

EFFECTS OF CLIMATE AND PREY AVAILABILITY ON FORAGING IN A SOCIAL SPIDER, *STEGODYPHUS MIMOSARUM* (ARANEAE, ERESIDAE)

T.E. Crouch: Department of Zoology and Entomology, University of Natal,
Pietermaritzburg, South Africa and Durban Natural Science Museum, P.O. Box 4085,
Durban 4000, South Africa.

Y. Lubin: Mitrani Department of Desert Ecology, Blaustein Institute for Desert
Research, Ben Gurion University of the Negev, Sede Boqer Campus, 84990 Israel

ABSTRACT. Tropical areas with favorable climatic conditions, high prey availability and large prey size are assumed to favor sociality in spiders. Notwithstanding, the three social species of *Stegodyphus* (Eresidae) inhabit arid and semi-arid habitats with marked daily and seasonal variation in climate. The nests of the social spider *Stegodyphus mimosarum* Pavesi commonly occur in dry Acacia savanna in southern Africa. We investigated the abiotic conditions to which the nests of *S. mimosarum* are exposed and the changes in availability of potential insect prey at different times of year and over the daily cycle. We used these data to determine the extent to which prey availability and climatic conditions explain seasonal and daily variation in the activity of the spiders. Data were collected during four sampling periods a year over two years from nests of *S. mimosarum* located on the Mkomazi River Bridge (KwaZulu-Natal, South Africa). We measured ambient and nest temperatures and in a sample of nests, spider growth rate, prey availability, foraging activity and activity on the web at night. Spiders had two periods of increased growth rate occurring in early and late summer, at times of year when ambient temperature rarely falls below 20 °C. Temperatures inside the nest were generally higher than ambient throughout the day and night. Foraging response, measured as the numbers of individuals responding to the vibrations of a tuning fork, was significantly higher by night than by day. In summer, foraging response decreased with increasing temperature during the day, whereas in winter, there was a positive correlation between foraging response and temperature at night. Potential prey, measured as mean numbers of insects trapped in a sample of webs, were more abundant during the day than at night, despite the fact that the spiders were most active on the web at night. Nocturnal insects, however, were larger than diurnal ones and spiders handled significantly more large prey both during the day and at night. Correlation and partial correlation analyses indicate that ambient temperature and windspeed play a direct role in influencing foraging and other activity on the web. Nonetheless, the predominance of nocturnal activity in both summer and winter could not be explained by climatic conditions and prey availability alone. Some other factor (e.g., predation or parasitism) may be involved.

Keywords: Climate, prey availability, foraging, social spider

Most of the 18 or so known species of social spiders (also referred to as cooperatively group-living or permanently social) are tropical, and most are found in the wet tropics (D'Andrea 1987; Avilés 1997). Sociality may occur with greater frequency in the tropics because the benign climate allows activity to be maintained year-round, and thus a colony can be maintained continuously over several generations, or because potential insect prey are available year-round, also allowing continuous activity (Riechert 1995). Additionally, large insects, which can be captured more ef-

ficiently by a group of spiders than by solitary spiders of a similar size (Nentwig 1985), are more abundant in the tropics (Rypstra 1990).

Notwithstanding, the three social species of *Stegodyphus* (Eresidae) (and indeed, most of the remaining 17 solitary species of the genus) are sub-tropical and live in arid, semi-arid and seasonally wet savannas of Africa and the Indian subcontinent (Kraus & Kraus 1988). The two African species, *S. dumicola* and *S. mimosarum*, occur largely in dry thornbush (Acacia) savanna, where summer temperatures are high and winter is generally cold,

with little plant growth or insect activity. *Stegodyphus* colonies have a strongly seasonal developmental cycle, which is linked to the local seasonal regime (Seibt & Wickler 1988). Consequently, we expect to find a strong correlation between variation in the physical and biotic environment and both daily and seasonal activity of spiders in *Stegodyphus* colonies. We investigated the abiotic conditions to which the nests of *S. mimosarum* are exposed at different times of year and the changes in availability of potential insect prey. We used these data to examine the hypothesis that prey availability and abiotic conditions explain seasonal and daily variation in the activity of these spiders.

METHODS

Natural history and study area.—Nests of *S. mimosarum* often occur near water, in the canopy of thorny acacia and other trees, as well as on man-made structures such as utility poles, road signs, fences and bridges (Kraus & Kraus 1988; Seibt & Wickler 1988; pers. obs.). Our study population consisted of nests that occupied the railing of the Mkomazi River bridge, 23 km west of Richmond in KwaZulu-Natal (29°54'31"S, 30°05'35"E). The bridge spans 66 m and is 8 m wide. The 354 vertical aluminum struts on each side of the bridge support a horizontal handrail at a height 1 m above the ground. The nests occupy the underside of the railing between the vertical struts along both sides of the bridge. At the start of the study in January 1995, there were 615 nests on both sides of the bridge combined. At this time these nests were at most nine years old, as the 1987 floods destroyed the railings together with any nests. Nests occurred also in the canopies of trees downstream from this site and on trees growing on pylons below the bridge. These latter nests were difficult to access.

The annual rainfall for the area for 1994 was 630 mm, 1041 mm for 1995 and 1112 mm for 1996. Most rain fell in summer (October–February). Summer temperatures regularly exceeded 35 °C and during winter dropped below 0 °C.

Data collection.—The study was conducted from January 1995 to November 1996. We measured body size (length from the tip of the prosoma to the tip of the abdomen) of individuals from 20–30 randomly selected nests

at different times of year. Measurements of abiotic and biotic factors were conducted over a 3-day period, once every 4 months (February, May, August, November). Forty to sixty nests were randomly selected for each observation period (20–30 nests from each side of the bridge). We measured nest, web and ambient temperatures, windspeed, spider activity and prey availability. Diurnal data were collected over three days during each month sampled in 1995. Nocturnal data were collected during two nights each in May and August 1996, and from a single night each during November and February (1996). Time of day is local time (GMT +2 hours).

Nest conditions: Temperatures were measured from a single nest on the south side of the bridge. Measurements were taken inside the nest, about 2 cm below the surface and 3 cm below the nest in the capture web on the north and south sides. These measurements were taken using copper-constantan thermocouples. A temperature probe and anemometer were placed at nest height to measure ambient temperature and windspeed respectively. Temperatures and windspeeds were recorded at three five-minute intervals every hour by an MCS120-02 datalogger (M C Systems, Steenberg, Cape Town, South Africa) and hourly means were then calculated and summarized separately for day and night periods.

Prey availability: Nests were surveyed at two-hour intervals for new prey items that were either trapped on the web or were being handled by the spiders. The numbers of spiders handling the prey, prey size (mm) and identity to order level were noted.

Foraging response: Foraging response was assessed as the number of spiders responding to the vibrations emitted from a musical tuning fork (440 Hz) which are similar to vibrations produced by buzzing insects trapped in the web (Henschel et al. 1992). The stimulus was applied to the capture web 4 cm below the nest. The number of spiders emerging from the nest or approaching the vibrating tuning fork within 5 seconds was counted at two-hour intervals throughout the observation period. This behavior provided a relative measure of the readiness of spiders to attack prey caught in the web and allowed us to compare the spider's response to a standardized stimulus under different ambient conditions.

Activity on the web at night: Spiders that

emerged from the nest at night were observed under red light. Activities on the nest surface and on the capture web included construction (spinning), maintenance (the removal of old prey and silk) and prey capture. In addition, some individuals were stationary on the nest surface or on the web. The number of spiders on the web and nest surface was recorded at two-hour intervals prior to measuring foraging effort with the tuning fork.

Statistical analysis.—Temperatures measured at different locations (inside the nest, on the web, ambient) were compared using paired *t*-tests (two-tailed) on the mean hourly temperatures for the three days or two nights of each sample period. Data for each month were tested separately both here and in all other comparisons. As the same null hypothesis was being tested on each of the three days sampled (e.g., nest temperature did not differ from ambient), a Bonferroni correction was used and the acceptable level of significance ($P = 0.05$) was divided by *k*, the number of non-independent tests ($k = 3$ and 2 for diurnal and nocturnal data, respectively) (Haccou & Meelis 1994). Chi-squared tests for independence were conducted for prey data where the variables included in the analysis were the type of prey (order), prey size classes and the number of spiders handling prey (Zar 1984).

Relationships between the variables (ambient temperature, windspeed, prey, foraging response and spider activity) were tested with Pearson's product-moment correlation and Spearman's rank correlation. Partial correlation analysis (Zar 1984) was used to determine the correlation between any two variables while maintaining all others constant.

Data on prey availability and foraging activity required logarithmic transformation prior to analysis and values were replaced by $\log(x + 1)$ (Elliot 1983).

RESULTS

Growth rate and seasonal development of spiders.—*Stegodyphus mimosarum* appeared as juveniles in February, were subadult from October to December, and reached maturity in summer from December to February when mating and egg laying took place (Fig. 1). Little growth occurred during the winter months (May to August). In 1996, individual growth during the winter months (May–July) was less than 5% per month (av-

eraging 1.7–4.3%, in body length), whereas in summer spiders grew 13.3–16.6% per month in body length.

Seasonal changes in temperature and windspeed.—*Diurnal conditions:* During February, which is late summer and the hottest month sampled, the temperature inside the nest was on average 2.5 °C higher than ambient ($t = 4.64$, $P < 0.001$) (Fig. 2). During February a maximum of 41.7 °C was recorded within the nest and 36.6 °C for ambient temperature. Temperatures below the nest, on the south and north sides of the railing, were not significantly different from ambient. However, they were on average 3.0 °C ($t = 5.65$, $P < 0.001$) and 2.8 °C ($t = 5.17$, $P < 0.0001$) respectively, lower than temperatures within the nest. At high ambient temperatures (± 30 –35 °C), spiders were observed sitting below the nest in a layer of loose silk on the nest surface, as well as just inside the nest entrances. Throughout the remainder of the year (i.e., May, August and November), temperatures measured inside the nest did not differ significantly from ambient, nor from those on the north and south side of the nest. However, temperatures within the nest were generally above those on the web. Maxima recorded for ambient and nest temperature were 33.2 °C and 37.7 °C, respectively for May, and 32.2 °C and 32.8 °C for November. Windspeed was highest during the summer months of November and February (Fig. 2).

Nocturnal conditions: During February and August nighttime temperatures within the nest were only slightly, but significantly higher than ambient (Fig. 2). Temperatures inside the nest were on average 1.0 °C higher than ambient ($t = 2.62$, $P = 0.01$) in February and 0.9 °C in August ($t = 2.50$, $P = 0.013$). In winter (May) and early summer (November) nest and ambient temperatures showed similar patterns, but they were not significantly different. Nest temperatures were at a minimum of 7.1 °C in August, when minimum ambient was 6.1 °C, and at a maximum of 27.7 °C in February, when maximum ambient reached 27 °C. Nighttime windspeed was highest in the summer months (November–February, Fig. 2).

Daily changes in temperature and windspeed.—Mean ambient and nest temperatures reach a maximum between 1200–1400 h and were at a minimum before sunrise (Fig. 3).

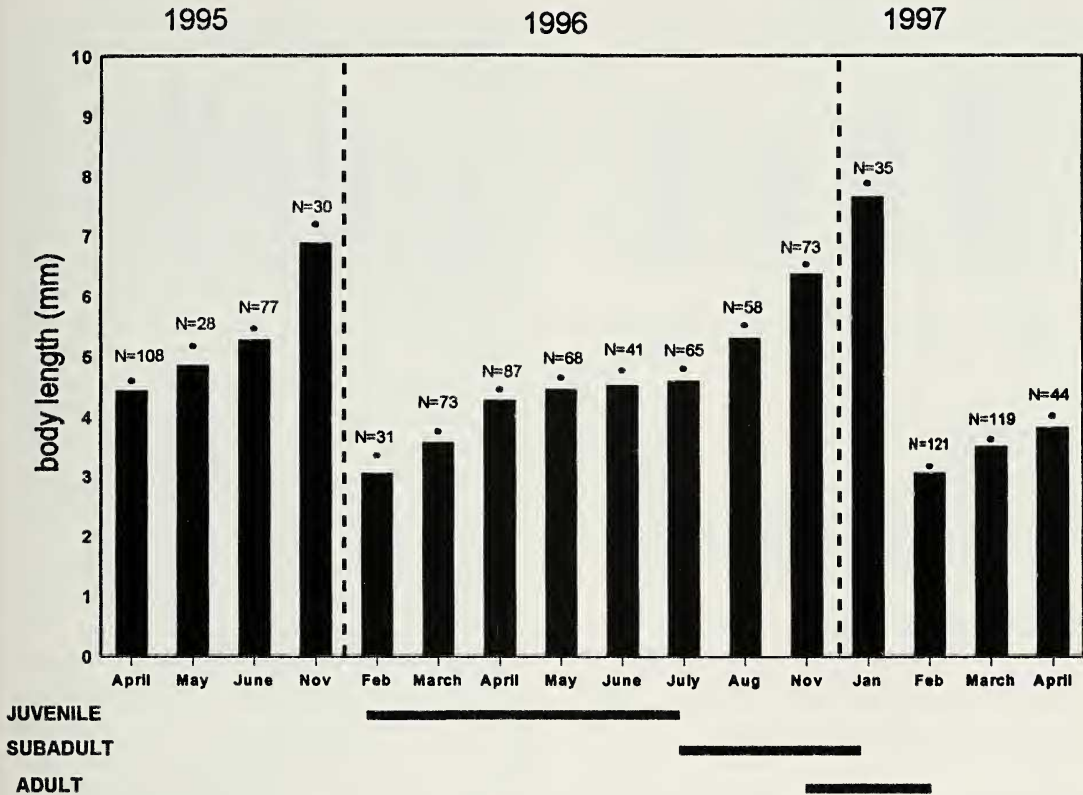


Figure 1.—Mean and 95% confidence intervals (dots above bars) for body length of *Stegodyphus mimosarum* and the period of occurrence of different life stages on the bridge.

During winter (May–August) the temperature differences between day and night were extreme, resulting in rapid loss of heat from the nest from midday to sunset, and rapid heat gain from sunrise to midday (Fig. 3). Nest and ambient temperatures in winter (August) remained well below 25 °C throughout the day. During the hottest month (February), temperatures inside the nest were above 30 °C from 1000–1400 h.

Daytime windspeeds peaked at 1600 h and were both greater and more variable than those measured at night. Wind and temperature were not significantly correlated, apart from nighttime records in February and May (Spearman rank correlation, $R = 0.465$, $P = 0.004$, $n = 36$ and $R = 0.374$, $P = 0.009$, $n = 75$, respectively).

Prey Availability.—*Prey numbers:* Throughout the year the greatest numbers of prey were found on the web between 0800–1000 h; the greatest numbers of prey per web were in the summer months (May–November;

Fig. 4). With the exception of November, very few prey items were observed in the webs during the night (1900–0500 h), despite the fact that the spiders were most active at this time (see below). In all months, more insects were trapped in *S. mimosarum* webs (= available prey) during the day than at night. A single insect was trapped at night in a survey of approximately 50 webs in each of the sampling months of February and August (late summer and late winter, respectively). In May (early winter) and November (early summer) respectively, 4% and 12% of the insects trapped were nocturnal. While these figures represent insects that landed on the web and were available to spiders, not all of these insects were actually captured by the spiders (Table 1). There was no significant difference between the numbers of insects actually handled by day and night. However, proportionally more nocturnal insects were handled (83% and 78% of trapped insects in May and November, respectively), whereas only 5–25%

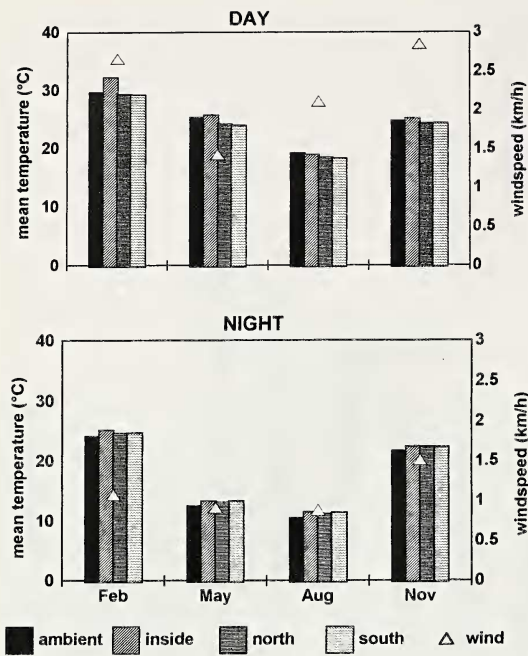


Figure 2.—Mean windspeed (km/h), ambient temperature (°C) and temperatures inside and below the nest on the north and south side.

of diurnal insects were handled by the spiders (Table 1).

We compared the sizes of insects trapped in the webs with those of prey actually handled by the spiders, and similarly, the types of insects trapped and handled. Because of small

sample sizes in some months, we pooled the data from all sampling dates for the statistical analyses.

Prey size: Most insects trapped in the capture webs were < 3 mm in body length (Table 1). Despite their availability, insects of this size class were rarely handled by the spiders. Medium sized prey (3–6 mm) and larger insects (> 6 mm) were handled significantly more often than expected from their abundance in the webs by day (all seasons combined, $\chi^2 = 164.8$, $df = 3$, $P = 0.0001$). A large proportion of the prey available at night was greater than 3 mm in length and there was no significant difference between the size of prey available and those handled at night (all seasons combined, $\chi^2 = 1.32$, $df = 2$, $P > 0.05$).

Prey type: The prey taxa available changed throughout the year. Diptera were common in all samples, Ephemeroptera were most common in February; Hemiptera and Coleoptera in May and November, and Hymenoptera in November (Table 2). There were significant differences in the distribution of major taxa available in the web and those handled by the spiders during the day (all seasons combined, $\chi^2 = 32.98$, $df = 4$, $P = 0.001$). By day, more Coleoptera and Diptera, and fewer Hemiptera, were handled than expected. Nocturnally, prey taxa available in the web and those handled by spiders did not differ statistically. Three-

Table 1.—The distribution of size classes of prey available to the spiders (insects trapped in webs) and the corresponding percentage handled by them.

| Size classes | February | | May | | August | | November | |
|---|----------|-------|------|-------|--------|-------|----------|-------|
| | Day | Night | Day | Night | Day | Night | Day | Night |
| Prey available in webs (%) | | | | | | | | |
| <1 to 3 mm | 58.1 | 0 | 64 | 33.3 | 37.2 | 100 | 80.9 | 7.3 |
| 3.1 to 6 mm | 19.3 | 100 | 12.8 | 50.1 | 37.6 | 0 | 16 | 21.8 |
| 6.1 to 15 mm | 19.3 | 0 | 20.5 | 8.3 | 25.5 | 0 | 2.7 | 56.4 |
| >15 mm | 3.2 | 0 | 2.7 | 8.3 | 0 | 0 | 0.4 | 14.5 |
| Total prey available | 31 | 1 | 326 | 12 | 43 | 1 | 406 | 55 |
| Prey handled (%) | | | | | | | | |
| <1 to 3 mm | 0 | 0 | 0.6 | 25.1 | 0 | 100 | 0.7 | 0 |
| 3.1 to 6 mm | 3.2 | 100 | 2.5 | 41.6 | 2.3 | 0 | 0 | 14.5 |
| 6.1 to 15 mm | 16.1 | 0 | 8.8 | 8.3 | 2.3 | 0 | 0.7 | 49.18 |
| >15 mm | 3.2 | 0 | 2.5 | 8.3 | 0 | 0 | 0 | 14.5 |
| Total prey available | 7 | 1 | 47 | 10 | 2 | 1 | 6 | 43 |
| Prey handled as % of total prey available | | | | | | | | |
| | 22.5 | 100 | 14.4 | 83.3 | 4.6 | 100 | 1.4 | 78.2 |

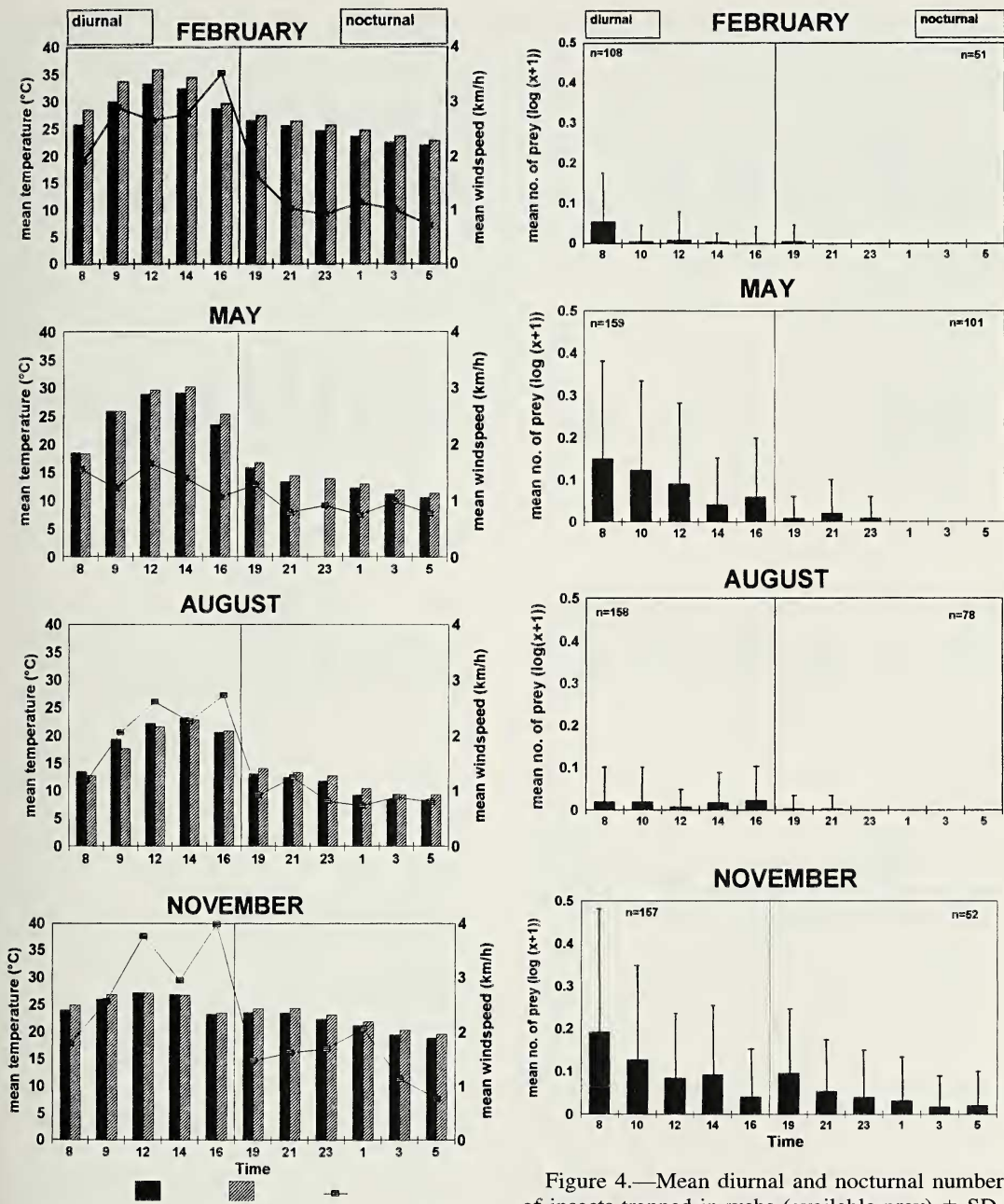


Figure 3.—Mean diurnal and nocturnal ambient temperature, nest temperature (°C) and windspeed (km/h).

Figure 4.—Mean diurnal and nocturnal numbers of insects trapped in webs (available prey) \pm SD.

way contingency tables (partial independence) tested for interactions between prey size and type for all seasons. We found for both day and night there was a lack of independence between prey size and type in influencing whether the prey was handled (day: $\chi^2 =$

197.6, $df = 8$, $P = 0.0001$; night: $\chi^2 = 15.58$, $df = 6$, $P = 0.016$).

Foraging response.—The response of spiders to a prey stimulus (tuning fork) was greater at night than during the day: February, $t = -17.3$, $P = 0.001$; August, $t = -4.2$, $P = 0.012$ and November, $t = -10.3$, $P = 0.001$ (Fig. 5). For all of these $P < 0.013$, the Bonferroni-adjusted level of alpha. Diurnal for-

Table 2.—The distribution of taxa of prey available to the spiders (insects trapped in webs) and the corresponding percentage handled by them.

| Prey type | February | | May | | August | | November | |
|----------------------------|----------|-------|------|-------|--------|-------|----------|-------|
| | Day | Night | Day | Night | Day | Night | Day | Night |
| Prey available in webs (%) | | | | | | | | |
| Coleoptera | 3.2 | 100 | 16.8 | 16.6 | 0 | 0 | 3.2 | 47.7 |
| Diptera | 29 | 0 | 49.6 | 50 | 76.7 | 100 | 13.3 | 10.9 |
| Hemiptera | 22.5 | 0 | 26.9 | 0 | 4.6 | 0 | 38.4 | 3.6 |
| Hymenoptera | 9.6 | 0 | 3.3 | 25 | 0 | 0 | 22.1 | 34.5 |
| Other | 35.7 | 0 | 4.3 | 8.4 | 18.7 | 0 | 23 | 3.3 |
| Total prey available | 31 | 1 | 326 | 12 | 43 | 1 | 406 | 55 |
| Prey handled (%) | | | | | | | | |
| Coleoptera | 3.2 | 100 | 2.7 | 8.3 | 0 | 0 | 0.2 | 38.1 |
| Diptera | 9.6 | 0 | 9.8 | 41.6 | 4.6 | 100 | 0.2 | 3.6 |
| Hemiptera | 0 | 0 | 1.2 | 0 | 0 | 0 | 0.4 | 1.8 |
| Hymenoptera | 9.6 | 0 | 0.3 | 25 | 0 | 0 | 0 | 32.7 |
| Other | 0 | 0 | 0.3 | 8.3 | 0 | 0 | 0 | 1.8 |
| Total prey handled | 7 | 1 | 47 | 10 | 2 | 1 | 6 | 43 |

aging response was higher in May than other months and spider activity was not significantly different by night and day ($t = -3.62$, $P > 0.013$). With the exception of February, foraging response decreased in the second half of the night, from about 0100 h. A similar pattern was observed when we used the proportion of nests in which spiders responded rather than mean number of spiders responding. The diurnal response levels varied considerably, with peaks occurring at different times of the day throughout the year (Fig. 5). February, May and August had higher response levels than November. This is at least in part attributable to the presence of young spiders in the nests during this period, whereas in November most spiders were subadult or adult; and the colonies contained fewer individuals owing to mortality during the growth phase.

Nocturnal activity on the web.—Shortly after sunset, spiders emerged from the nest and dispersed over the nest surface and capture web where they engaged in web cleaning, construction, or were motionless on the nest or web. The numbers emerging from the nests were highest between 0300–0400 h in February and November (summer) and between 1900–2100 h during the winter months (May and August) (Fig. 6). All spiders returned to the nest shortly before sunrise.

Relationships between activity, prey availability and abiotic factors.—Foraging

response was correlated with climatic variables and prey availability in some instances and not in others (Table 3). By day foraging was negatively related to windspeed in all four sampling periods, with the probability of $0.5^4 = 0.063$ of a negative relationship occurring by chance alone in all four samples. There was no significant correlation between foraging response and windspeed at night. Daytime foraging response was negatively correlated with ambient temperature in November (summer), while at night foraging response showed a strong positive correlation with ambient temperature in August, which was the coldest month. Prey availability and foraging response were significantly positively correlated only in February (daytime sample), however all 6 correlation coefficients were positive, with a probability of this occurring by chance alone of $0.5^6 = 0.016$.

Partial correlation analysis allowed for the comparison of two variables whilst holding constant the influence of other variables on the two in question. These results show a similar pattern to that obtained for the simple correlation (Table 3). Spider activity on the web at night was positively correlated with ambient temperature in August, as was the foraging response at night, and foraging response and activity were strongly positively correlated. During August the partial correlation coefficients for both foraging response and spider activity with ambient temperature were positive and

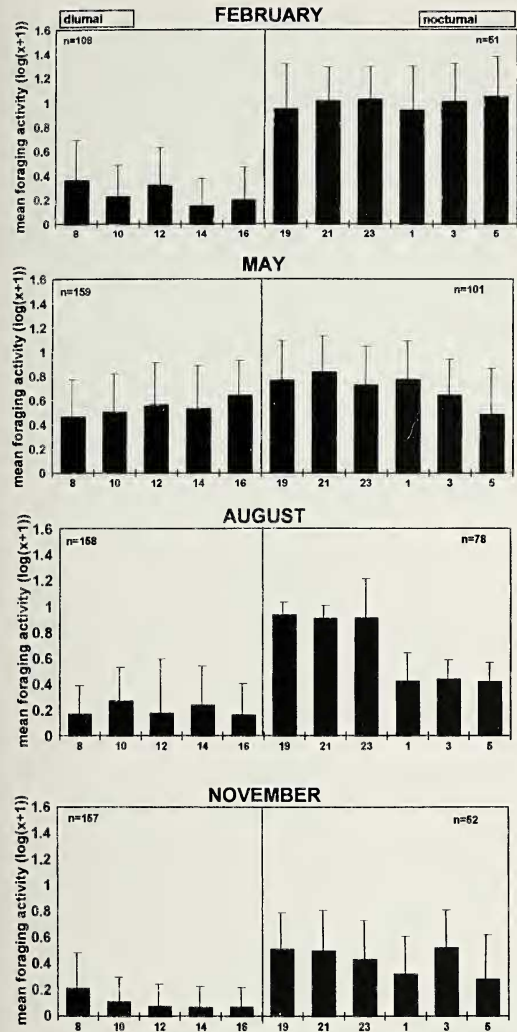


Figure 5.—Mean diurnal and nocturnal spider foraging activity (number of spiders approaching vibrating tuning fork in 5 seconds) \pm SD.

significant, suggesting that nighttime activity is strongly dependent on ambient temperature during the cool season.

DISCUSSION

Seasonality of spider growth.—The seasonality of growth and the range of spider sizes observed here was similar to those of colonies observed in other parts of KwaZulu-Natal (unpubl. data) and by Seibt & Wickler (1988). There was little spider growth in winter (May, August), when very small young were present in the nest and after the females had died. Growth to maturation and egg-laying occurred in the summer months.

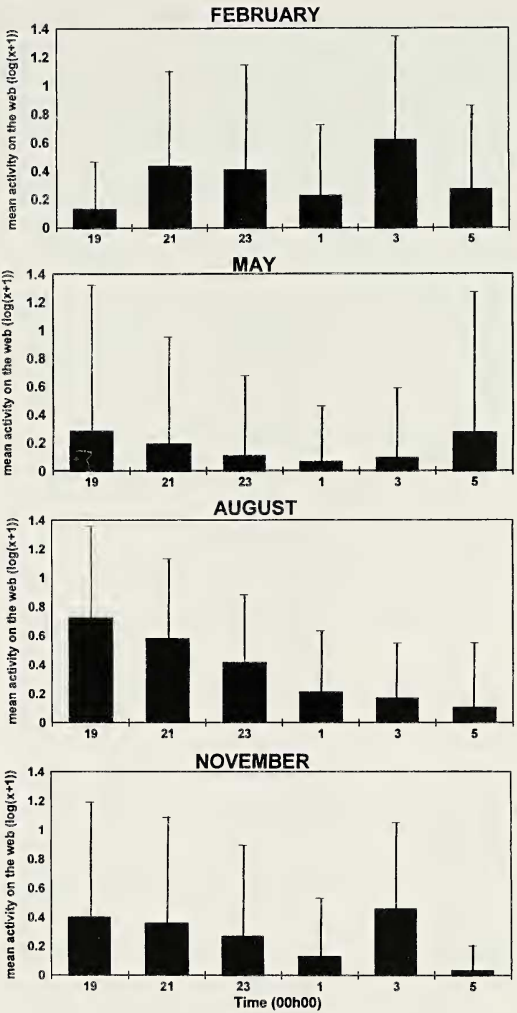


Figure 6.—Mean number of spiders on the web at night \pm SD.

The difference in the growth rate of spiders during winter and summer months corresponds to the initial slow increase and the exponential phase, respectively, of a typical sigmoid growth curve. The food requirements of a colony are expected to be greatest during the period of exponential growth of juveniles, i.e., during early summer. Consequently, conditions should be more favorable for growth in the summer months. This was largely the case for the abiotic conditions as well as the availability of prey.

Abiotic conditions: In May and August, mean nest temperatures were below 25 °C during the day and less than 15 °C at night. February was the hottest month and in both

Table 3.—Correlations (Pearson's) between mean number of spiders responding to prey stimulus (foraging), insects trapped on 40–60 webs (prey), nocturnal activity on the web (On web), wind and ambient temperature (T_{amb}). the following symbols have been used: only one prey item was recorded in night samples and therefore omitted from the analysis (*), appropriate for nocturnal data only (**), activity on the web was not included in the analysis of foraging response (***), significant partial correlations coefficient ($P \leq 0.05$)(§).

| | | Correlation coefficient (P -value) | | | |
|------------------------|-------------|---------------------------------------|------------------------------|--------------------------|--------------------------|
| | | Wind | T_{amb} | Prey | On Web** |
| February | | | | | |
| Day ($n = 15$) | Foraging | −0.054 (NS) | −0.387 (NS) | 0.652§ ($P < 0.01$) | — |
| | Prey | −0.040 (NS) | −0.506§ ($P \leq 0.05$) | — | — |
| Night* ($n = 6$) | Foraging | −0.824§ ($P < 0.05$) | −0.479 (NS) | — | 0.526 (NS) |
| | On Web | −0.503 (NS) | −0.371 (NS) | — | — |
| May | | | | | |
| Day ($n = 14$) | Foraging | −0.467§ ($P = 0.09$) | 0.161 (NS) | 0.046 (NS) | — |
| | Prey | −0.253 (NS) | −0.472 (NS) | — | — |
| Night ($n = 12$) | Foraging | 0.356 (NS) | 0.497 (NS) | 0.493 (NS) | 0.493 (NS) |
| | Prey | 0.215 (NS) | 0.429 (NS) | — | — |
| | On Web | 0.438 (NS) | 0.267 (NS) | 0.348 (NS) | — |
| August | | | | | |
| Day ($n = 15$) | Foraging | −0.036 (NS) | 0.050 (NS) | 0.077 (NS) | — |
| | Prey | −0.182 (NS) | −0.188 (NS) | — | — |
| Night* ($n = 12$) | Foraging | 0.421 (NS) | 0.955§ ($P < 0.001$) | — | 0.898 ($P < 0.001$) |
| | On Web | 0.476 (NS) | 0.961§ ($P < 0.001$) | — | — |
| November | | | | | |
| Day ($n = 18$) | Foraging | −0.529§ ($P \leq 0.05$) | −0.452§ ($P \leq 0.05$) | 0.326 (NS) | — |
| | Prey | −0.349 (NS) | 0.074 (NS) | — | — |
| Night ($n = 6$) | Foraging*** | 0.098 (NS) | 0.516 (NS) | 0.472 (NS) | — |
| | Prey | 0.294 (NS) | 0.829§ ($P \leq 0.05$) | — | — |
| | On Web | 0.095 (NS) | 0.431 (NS) | 0.399 (NS) | — |

February and November nighttime temperatures rarely fell below 20 °C. Although the nests were positioned on an exposed bridge, strong winds were not recorded during our observation periods. The windspeed was generally lower in the winter months of May and August and higher during November, both during the day and night. Nest and ambient temperatures peaked between 1200–1400 h and were lowest just before dawn. While the difference between day and nighttime nest temperatures was often > 15 °C during the winter months, in November there was little

difference between the maximum and minimum nest temperatures recorded (± 5 °C).
Temperatures inside the nest were nearly always higher than ambient, as found also by Seibt & Wickler (1990). Thus, in the summer months, spiders inside the nest might suffer excessive heat loads during mid-day, but they can cool convectively by moving out of the nest. Convective cooling may be enhanced by the prevalence of stronger afternoon winds during the summer months. Seibt & Wickler (1990) showed that *S. mimosarum* actively avoided temperatures above 41 °C. During

one hot day in December 1997, when ambient temperature exceeded 42 °C at 0900 h, we observed spiders moving onto the web into the shadow cast by the nest, and some females moved their egg sacs onto the web as well. This behavior was observed frequently in the social *S. dumicola* (Seibt & Wickler 1990; pers. obs.). A similar response to high mid-day nest temperatures occurs in the solitary *Stegodyphus lineatus* (Henschel et al. 1992) and in a widow spider *Latrodectus revivienis* (Lubin et al. 1993), both web-building species of desert habitats. In all of these cases, the silken structure of the nest does not protect the spiders from high daytime temperatures (see also Seibt & Wickler 1990), rather the spiders must use behavioral methods of thermoregulation.

Prey availability: Although insect abundance was highest during the day, the response of spiders to web vibrations (simulated prey) was greater at night. Furthermore, spiders handled a greater proportion of insects trapped at night than during the day. Nocturnal insects constituted only 8% of the total number of insects available on the web, but 47% of the prey actually handled by the spiders. The distribution of insect sizes suggests an explanation for this anomaly: more than half of the diurnal insects trapped were very small (< 3 mm body length), whereas more than half of the nocturnal insects were > 6 mm. Using an approximate conversion for insect body length to biomass (mass = $0.0305 \times \text{length}^{2.62}$; Rogers et al. 1976), we estimated that nocturnal insects constituted 28% of the biomass of available prey and 46% of the biomass of insects handled by the spiders. Thus, in terms of energy intake, nocturnal insects were more profitable than diurnal prey.

The prey taxa available changed throughout the year; and there were significant differences in the distribution of major taxa available in the web and those handled by the spiders, suggesting that the spiders fed selectively. Owing to the lack of independence between prey type and prey size in our data, we cannot determine whether selection was for particular types or size classes of prey, or both factors combined. Ward (1986) analyzed prey remains from nests of *S. mimosarum*, finding similar seasonal differences in composition as well as a predominance of large prey items (beetles and orthopteroid insects). Prey exoskeletons may

bias the results toward the larger insects, which are less likely to become fragmented. Thus, our observations of prey handled by the spiders confirm Ward's conclusion, that *S. mimosarum* preferentially takes large prey, even when most insects available are small.

Foraging activity as a function of climatic conditions and prey availability.—Both web maintenance and prey capture occurred mainly at night. This strong diel pattern of activity could not be explained by climatic conditions and prey availability alone. Another important factor might be the risk of predation or parasitism. From September to February substantial mortality occurred in colonies, largely from parasitism by *Pseudopompilus funereus* (Hymenoptera, Pompilidae) (pers. obs.). Predation by a Red-billed Woodhoopoe (*Phoeniculus purpureus*) was observed on a colony of *S. mimosarum* at a different site. Both of these predators are diurnal.

Ambient temperature played a direct role in foraging and web-maintenance activities, while wind appeared to have less of an influence. Humidity inside and outside the nest was not measured, but may influence activity as well. Typically, low humidity and high ambient temperatures would coincide during midday (see Seibt & Wickler 1990). High ambient temperatures during the day reduced foraging response, as did low nighttime temperatures. In August, the coldest month, there was little nocturnal activity. Similarly, in *S. lineatus*, both the speed and frequency of responses to a prey stimulus (tuning fork) was lower at low ambient temperatures (Henschel et al. 1992). Another solitary eresid, *Seothyra henscheli*, from the Namib desert, showed very limited foraging response at temperatures below 20 °C. In general, spiders adapted to hot climates, may be constrained more by low ambient temperatures than high ambient temperatures, especially if foraging activity is largely nocturnal, as is the case in *S. mimosarum*. However, above-ambient temperatures inside the nest at night may act to buffer the low ambient temperature and thereby increase the time available to the spiders for foraging activity in cold winter months. Furthermore, large nests with greater thermal mass are better buffered against low temperature effects (Weldon 1997). Small colonies and newly established nests, however, may be sensitive to

immediate climatic conditions, as well as to the indirect effects of climate on prey availability.

One of the consequences of low temperatures at the start of the post-winter growth phase is its potential to delay maturation. In the solitary *S. lineatus*, delayed maturation has a strong negative effect on fitness, as the occurrence of wasp parasitism increases with time in the season and juvenile survival decreases if emergence is delayed (Henschel et al. 1992; Schneider & Lubin 1997; Ward & Lubin 1993). In the latter species, the width of the window of time for development is determined by climatic factors. Long-term monitoring of changes in numbers and sizes of colonies of *S. mimosarum* will provide information on the extent to which growth and survival vary with changing biotic and abiotic conditions.

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